

Cave-dwelling fauna of Costa Rica: current state of knowledge and future research perspectives

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Abstract

This study focused on the cave fauna of Costa Rica, which has remained relatively understudied despite the presence of more than 435 recorded natural caves and artificial subterranean sites. We collected and reviewed all available literature data on cave fauna in Costa Rica and created the first comprehensive review of the existing information. In addition, we report new records from field surveys conducted between 2015 and 2018. This study reported approximately 123 animal species, whereas the remaining records ($n = 82$) represented taxa that could not be identified at the species level. Data were collected from 127 locations throughout the country, with new cave fauna records from 41 sites. Notably, we reported the first occurrence of the true bug *Amnestus subferrugineus* (Westwood 1837) within Costa Rican caves, which represents an addition to the country's faunal inventory. As this study highlights the knowledge gaps in the subterranean fauna, it will serve as an important stepping stone for future research and conservation efforts related to caves in Costa Rica.

Keywords

cave fauna, caves, Central America, inventory, karst

Introduction

Caves are important habitats and roosts for a large number of animal taxa, such as bats and other highly specialized organisms, adapted to specific conditions, which usually consist of the absence of light, high humidity, and almost constant temperature (Romero 2009). Because of their isolation from the surface and other subterranean systems across evolutionary time, caves can provide refuge for numerous endemic species in a confined area, making them intriguing subjects for research (Culver and Pipan 2009). Tropical regions are fascinating for biospeleological research because of their high biodiversity and the presence of large underground systems (Deharveng and Bedos 2012). Despite the recent rapid progress in the study of cave-dwelling organisms in tropical regions such as Brazil (Campos-Filho et al. 2023), numerous areas and taxonomic groups remain underexplored (Niemiller et al. 2018 and Wynne et al. 2021). With its diverse and relatively understudied cave-dwelling fauna, Central America has enormous potential for speleological discoveries (Day and Koenig 2002; Taylor et al. 2011; Pacheco et al. 2020). Expanding research efforts in these areas is essential to better understand the unique biological communities in caves and their ecological roles.

Costa Rica is a small country located in the Neotropical region. It is a natural bridge between North and South America, and has been estimated to hold at least 5% of the world's biodiversity (Avalos 2019). Despite the existing knowledge, this country has great potential for taxonomic investigation and discovery. The country has a limestone surface area of approximately 430 km² with numerous karst landscapes and more than 435 described caves (Ulloa et al. 2011; Grupo Espeleológico Anthros 2023). Although the carbonated platforms in Costa Rica cover less than 1% of the country's area, several karstic systems exceed a kilometer in length (Ulloa 2009a). In addition to limestone caves, Costa Rica has several volcanic caves with a total length of 2.2 km (Ulloa and Alvarado, personal communication). The dimensions of the largest cave systems in Costa Rica are modest compared with those in other parts of Central and South America. However, Costa Rican caves are undoubtedly captivating research objects that have been attracting numerous expeditions since the first speleological explorations in 1943 (Goicoechea 2015).

The earliest records of cave fauna in Costa Rica were from 1965 to 1969, with studies on some cave-dwelling bat species (Armstrong 1969). Long-term research on Seba's short-tailed bats (*Carollia perspicillata*) was conducted in the late 1970s and the early 1980s in Santa Rosa National Park (Heithaus and Fleming 1978; Fleming and Heithaus 1986). Costa Rican caves grabbed the attention of the US National Speleological Society (NSS) and different European speleological groups, and several expeditions were conducted in the country, providing a tremendous scientific contribution (Hempel 1989; Peacock and Hempel 1993). Several dedicated biospeleological studies have been conducted in the country, with one describing a new species of stygobiont (Hobbs 1991). The existing biospeleological data are summarized in the book "Introduction to Speleology" (Alpizar et al. 2006). Cave-dwelling bats have been the topic

of recent studies (Cubero and Artavia 2016; Deleva and Chaverri 2018; Mitchell et al. 2018). Unfortunately, all previous efforts have covered only a portion of caves in the country. Many caves and taxonomic groups remain unknown.

This study aimed to provide an overview of the current state of knowledge regarding the cave-dwelling fauna of Costa Rica. Given that previous efforts have provided valuable, albeit scattered, information, we sought to systematize the existing data on the cave fauna of Costa Rica and add original preliminary research from our field expeditions. We hope that this study will provide insights for new studies and conservation efforts in Costa Rican cave-dwelling animals.

Methods

Literature review

We searched for literature sources that mentioned cave-dwelling fauna in Costa Rica, including but not limited to peer-reviewed articles, expedition reports, conference papers, short notes, and dissertations. We conducted searches using Google Scholar, Web of Science, and ResearchGate. We searched separately using each of the keywords “cave,” “underground,” “subterranean,” “cave fauna,” “speleology,” “trogllobiont,” “trogllobite,” “stylobiont,” “stylobite” in combination with the keyword “Costa Rica,” using the Boolean operator “and.” We examined the references in the articles obtained during the search for additional relevant sources. We searched for studies published in Spanish by translating the keywords and performing the search with the same word combinations. Furthermore, we checked the expedition reports of the Anthros Speleological group (Grupo Espeleológico Anthros 2023) and the archives of the University of Costa Rica's library (UCR 2023). The last search was performed in October 2022.

Field research

In addition to the literature review, we also included preliminary data from observations of cave-dwelling animals during speleological expeditions between December 2015 and August 2018. The research sites included natural caves, artificial tunnels, and abandoned mines. We used direct observations inside the roosts where the specimens were documented with photographs. Field guides were used to identify animals at the species level (Henderson 2011). A small number of invertebrates was collected and preserved in 96% ethanol. The collected material was distributed for further identification among specialists in the different taxonomic groups. Bats were divided into two categories, following the assessment of Sagot and Chaverri (2015): 1) cave-dependent – only known to roost in caves or cave-like structures, and 2) not cave-dependent – roosting in caves as well as in other types of roosts. We created a dataset for each record of cave-dwelling fauna, which included the following attributes: location, site type, protected area name (if applicable), conservation status of the species, and citation (if applicable).

Spatial data

We used GIS software (ArcGIS Desktop 10.8.1) to create the maps. The locations of the sites were obtained from the database of the Anthros Speleological Group (Grupo Espeleológico Anthros 2023). We included information on the origin of each subterranean site: karst, volcanic, marine, artificial or unknown. We used publicly available geospatial data from the National Geographical Institute to determine whether the sites were located in protected areas (SNIT 2023). Because of the sensitive species inhabiting the subterranean sites, we did not disclose the exact coordinates of each cave, as unregulated visitation may further affect these sensitive resources. Therefore, we plotted site locations at a low resolution following the best practices for generalizing sensitive species occurrence data (Chapman 2022).

Conservation status

We determined the management status of all species identified by cross-checking each species with the IUCN Red List (IUCN 2023b), appendices of the Convention on the Conservation of Migratory Species of Wild Animals (CMS Convention 2023), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2023), and the Costa Rican Law for the protection of wildlife (Ley de Conservación de Vida Silvestre, MINAE 2017).

Results

We identified a total of 62 sources reporting organisms in Costa Rican caves. Data from the published sources contained 773 records, with 123 unique organisms identified at the species level. The articles and reports were written in Spanish (33), English (25), French (4), and Italian (1). Of these, one-third (23) were peer-reviewed, and the earliest study was published in 1965. The majority of the studies (43) were published after 2003. Our study included 186 observations (both vertebrates and invertebrates) from 42 sites, four of which had no prior biospeleological records. The combined literature data and field research provided information for 127 locations, accounting for 30% of the 435 described subterranean sites in Costa Rica.

Conservation status of Costa Rican caves and cave-dwelling fauna

Regarding the level of protection, most sites (91) were located outside of protected areas. The categories of the protected areas were national park (25), national wildlife refuge (4), forestry reserve (2), and protected zone (2) (Fig. 1). The subterranean sites across the country's specific administrative regions, also known as "Conservation Areas", were distributed as follows: Osa (63), Central Region (16), Tempisque (16), Guanacaste (7), Huetar Norte (6), La Amistad Pacifico (6), Pacifico Central (4), Arenal Tempisque (3), La Amistad Caribe (2). Most sites were concentrated in the two

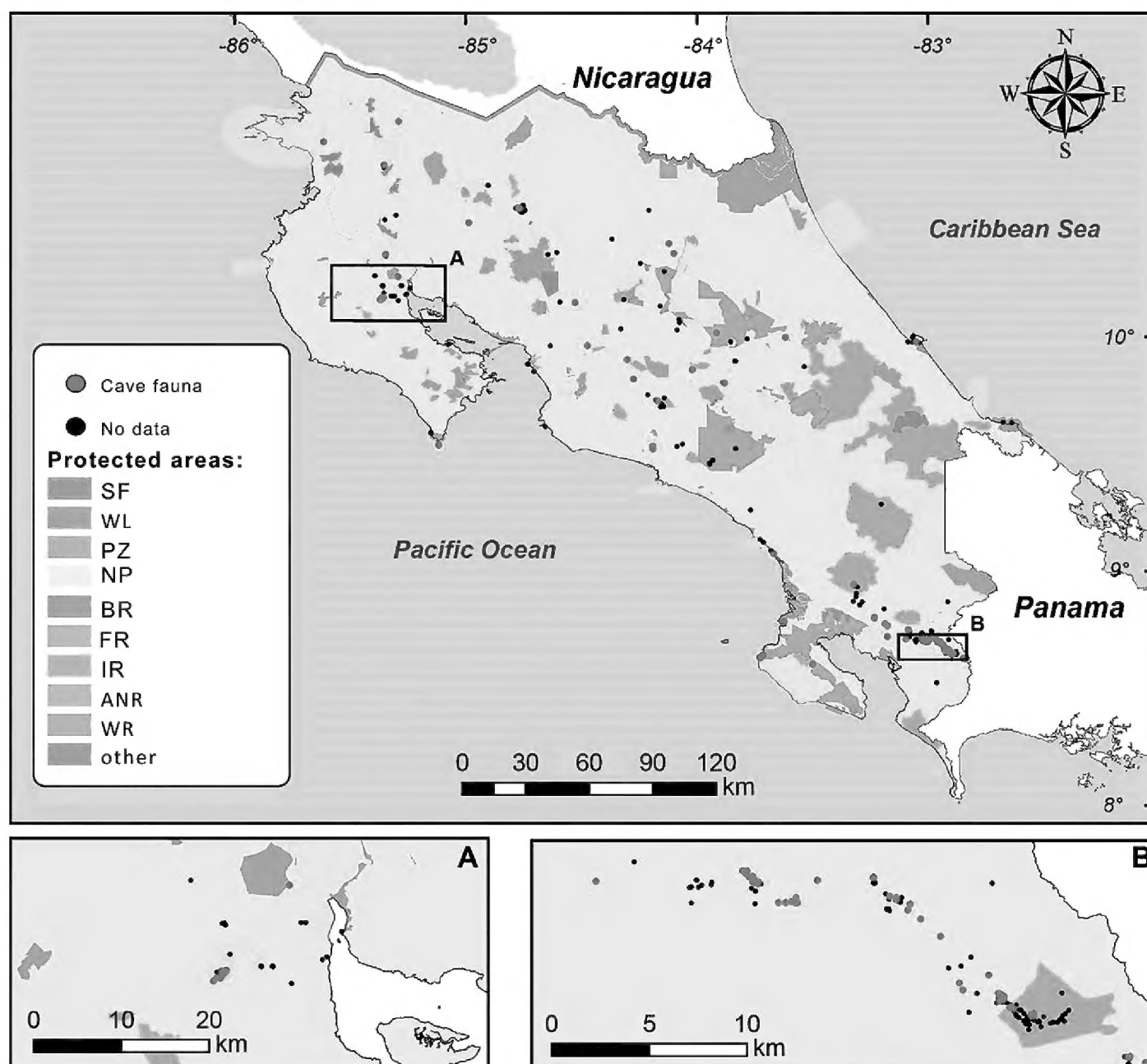


Figure 1. Costa Rica's subterranean sites: sites with records of cave fauna (red) vs. sites without records of cave fauna (black). The state-protected areas are presented in different colors: state farm (SF), wetland (WL), protected zone (PZ), national park (NP), biological reserve (BR), forest reserve (FR), indigenous reserve (IR), absolute natural reserve (ANR), and wildlife refuge (WR). The maps inserted at the bottom represent two karstic areas in Costa Rica with the most significant clusters of caves **A** Barra Honda karst area and **B** Zona Sur karst area.

largest karst areas in the country: Barra Honda, which is located in the Tempisque Conservation Area (Fig. 1A), and the Zona Sur Karst Area in the Osa Conservation Area (Fig. 1B). Fifteen of the 16 sites in Barra Honda were located within the borders of the Barra Honda National Park; only five of the 63 sites in Zona Sur had some level of state protection. Data on the of six of the sites were unavailable.

The distribution of global IUCN Red List conservation status among the species of cave-dwelling fauna was: "Least Concern" (75), "Not Evaluated" (43), "Data Deficient" (3), "Vulnerable" (2). Five species were included in the appendices of the CITES Convention. The Costa Rican Law for Wildlife Protection included nine species listed as "Reduced or Threatened population" and one species listed as "Endangered." No species were included in the appendices of the CMS Convention. The conservation status of all species is presented in Tables 1–3 and Suppl. material 1.

Faunistic diversity in Costa Rican caves

Approximately 123 animal species were recorded in Costa Rican caves, along with 82 other records that could not be identified at the species level. Bats (Chiroptera) were the most studied vertebrate group with 36 species, followed by 26 species of other mammals (e.g., opossums, rodents, or cats), 11 reptiles (Reptilia), and eight amphibians (Amphibia). Additionally, seven species of cave-dwelling fish (Actinopterygii) were identified. Only three species of birds (Aves) were observed in caves. Studies on invertebrate diversity were predominantly represented by insects (Insecta) with 81 reported taxa, followed by 43 arachnids (Arachnida), 11 springtails and bristletails (Entognatha), eight crustaceans (Malacostraca), and several other unique taxa, including snails, millipedes, clitellate worms, mollusks, centipedes, copepods, various worms, bristle worms, garden centipedes, and flatworms, each represented by one or a few species (Fig. 2).

Invertebrates

Mollusca

Snails and slugs (Gastropoda) were reported from 11 sites, and shellfish (Bivalvia) from one marine cave. Snails from the subfamily Subulininae have been observed in Costa Rican caves. The only species of snail identified at the species level was the miniature Awlsnail (*Subulina octona* (Bruguière, 1789)), which was observed in an abandoned gold mine in the Osa Peninsula.

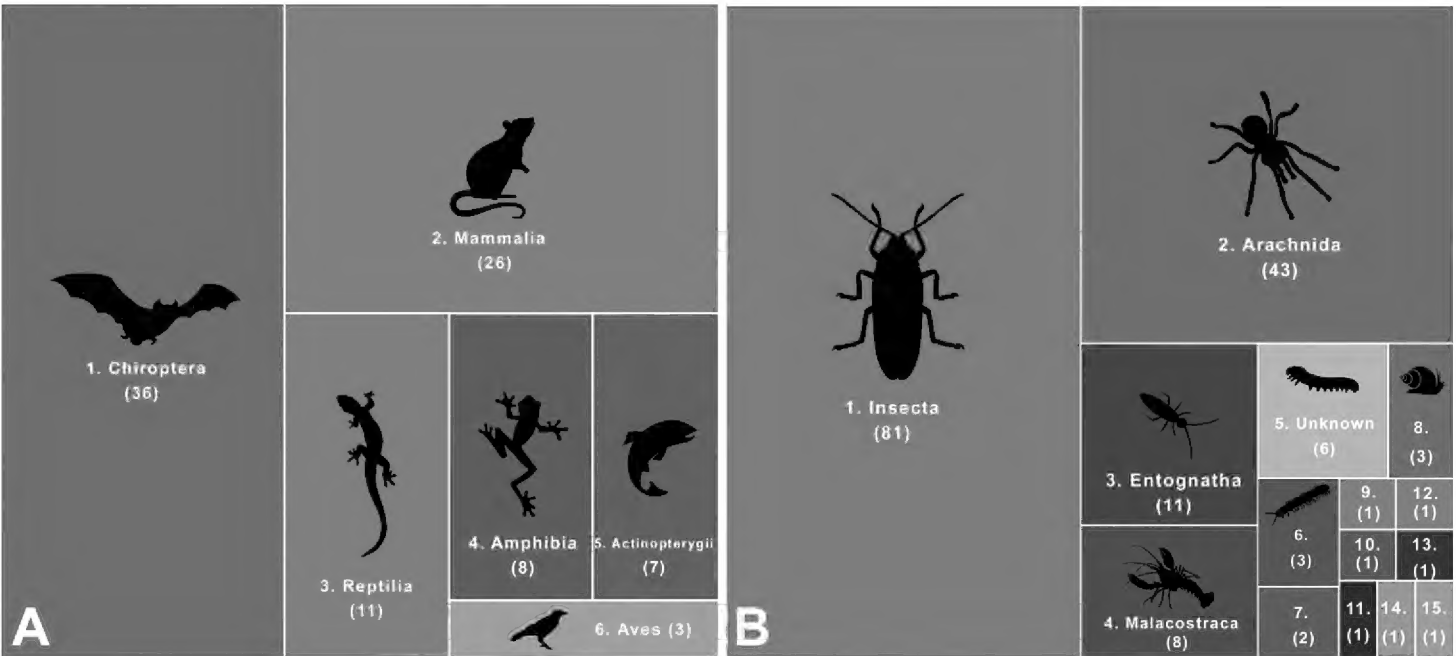


Figure 2. Number of animal taxa reported from subterranean sites in Costa Rica **A** vertebrates: 1. Chiroptera, 2. Mammalia (excluding bats) 3. Reptilia 4. Amphibia 5. Actinopterygii 6. Aves **B** invertebrates: 1. Insecta 2. Arachnida 3. Entognatha 4. Malacostraca 5. Unknown 6. Diplopoda 7. Clitellata 8. Gastropoda 9. Bivalvia 10. Chilopoda 11. Thecostraca 12. Oligochaeta 13. Polychaeta 14. Symphyla 15. Turbellaria.

Crustacea

Subterranean crustaceans included *Macrobrachium carcinus* (Linnaeus, 1758) (Fig. 3A), *Potamocarcinus magnus* (Rathbun, 1896), and *Ptychophallus montanus* (Rathbun, 1898). The troglophilic freshwater crab *Pseudothelphusa puntarenas* (Hobbs, 1991) from the Emus cave is currently the only known cave-dwelling species described from Costa Rica (Fig. 1B). Although it does not have any external troglomorphic modifications, the crab was observed only underground. The other crustaceans observed belonged to the classes Copepoda and Malacostraca (Bathynellacea and Isopoda) (Fig. 3C). A single observation of goose barnacles (*Pollicipes elegans* (Lesson, 1831)) (Fig. 3D) was reported from a marine cave.

Arachnida

A minimum of 16 mites and ticks (Acari) were identified (Table 1). The reported species of mites belong to the superfamily Hydrachnellae and the families Arrenuridae, Limnesiidae, Omartacaridae, and Torrenticolidae of the order Trombidiformes. Other identified mites belonged to the families Ascidae, Dinychidae, Macronyssidae, Spinturnicidae, Uropodidae (order Mesostigmata), and Torrenticolidae (order Trombidiformes). Several studies mentioned ticks and mites only at the order or family levels.

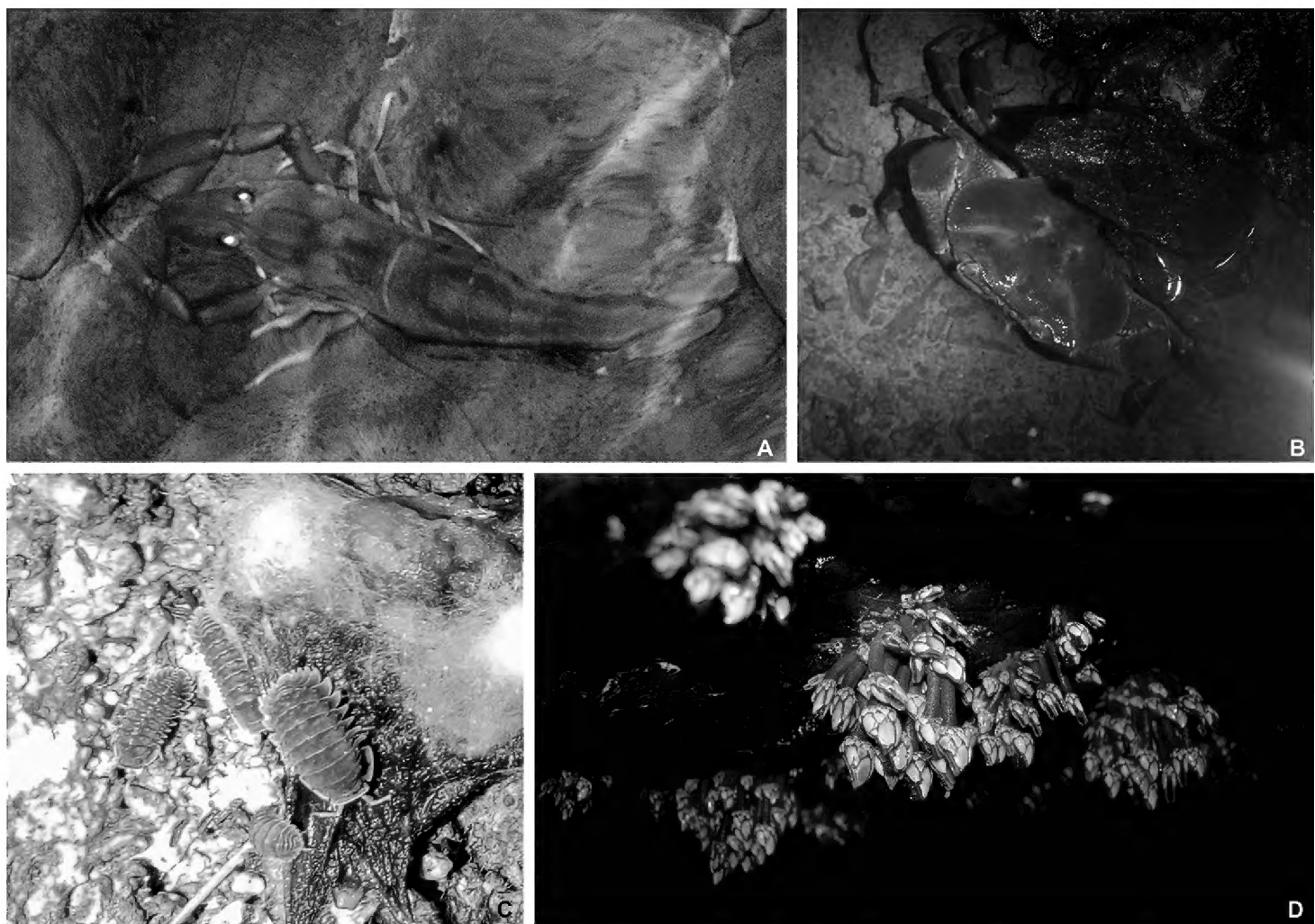


Figure 3. Crustaceans from Costa Rican caves **A** bigclaw river shrimp (*Macrobrachium carcinus*) **B** freshwater crab from Emus cave (*Pseudothelphusa puntarenas*) **C** woodlice (Armadillidae) **D** goose barnacles (*Pollicipes elegans*).



Figure 4. Arachnids in Costa Rican caves **A** wandering spider (*Ancylometes bogotensis*) with an egg sack **B** tarantula (Theraphosidae) **C** tailless whip scorpions (Phrynidae).

Spiders (Araneae) were often observed in caves, but we could not find relevant peer-reviewed publications on their diversity. We report observations of spiders in the families Attidae, Ctenidae, Dysderidae, Lycosidae, Theraphosidae, Theridiidae, Theridiosomatidae, and Trechaleidae (Fig. 4). Harvestmen (Opiliones) consisted of two identified species, *Pachylicus hispidus* Goodnight & Goodnight, 1983 from the family Phalangodidae and *Panopiliops inops* Goodnight & Goodnight, 1983 from the family Zalmoxidae. Both species were reported from the Damas cave. The remaining records (10) only mention the order without providing further details.

False scorpions (Pseudoscorpiones) were reported from five Costa Rican caves, but none of the reviewed studies provided species-level information. True scorpions (Scorpiones) were reported from three caves, and short-tailed whip scorpions (Schizomida) were observed in five caves in the Puntarenas region.

Records from 27 caves and subterranean sites mentioned Amblypygi, and there is a cave named after this animal (the Amblipigio cave). Cave-dwelling Amblypygi were reported to belong to the family Phrynidae, with one record of Tarantulidae. The second family was not mentioned in other sources and may refer to *Phrynus parvulus* (Pocock, 1902) of the family Phrynidae, previously known as *Tarantula marginemaculatus*. All Amblypygi in Costa Rica belong to the family Phrynidae, within the genera *Paraphrynus* (Moreno, 1940) and *Phrynus* (Harvey 2019). The identified species of cave-dwelling whip scorpions was *Paraphrynus laevifrons* (Pocock, 1894).

Myriapoda

Millipedes (Diplopoda) and centipedes (Chilopoda) were observed in at least 19 caves, but there were almost no data on their taxonomy, except for one record mentioning the family Polyxenidae. Garden centipedes from the class Symphyla were recorded from two caves.

Insecta

The reported species of cockroaches (Blattodea) were *Blaberus giganteus* (Linnaeus, 1758) and *Megaloblatta blaberoidea* (Walker, 1871). A noteworthy refuge for

cockroaches was the Hediondo cave, which harbors a large number of cockroaches from the *Blaberus* genus. Beetles (Coleoptera) from the families Alleculidae (Tenebrionidae), Bostrichidae, Carabidae, Cerambycidae, Curculionidae, Cleridae, Passalidae, Scarabaeidae, Scolytidae, Staphylinidae, and Tenebrionidae were observed inside Costa Rican caves and near their entrances. The Lamiinae subfamily and Clytini tribe of the Cerambycidae family, *Temnocheila* sp. (Trogossitidae), *Pyrophorus* sp. (Elateridae), and *Zophobas atratus* (Blanchard, 1845) (Tenebrionidae) were the only beetles classified at a lower taxonomic level. Cave crickets were observed on cave walls, but the available records only refer to them by their common names.

Bugs (Auchenorrhyncha) belonging to the families Fulgoridae and Cicadellidae were documented in Barra Honda National Park. True bugs (Heteroptera) from the families Reduviidae, Pentatomidae, Lygaeidae, Coreidae, Corixidae, and Cydnidae were reported to inhabit caves. Based on the specimens we collected during our field trips, we present the first record of the true bug *Amnestus subferrugineus* (Westwood 1837) (Heteroptera: Cydnidae) for the fauna of Costa Rica (Fig. 5). This is the first record of the genus *Amnestus* Dallas, 1851 in Costa Rican caves.

A few earwigs (Dermaptera) were mentioned in expedition reports from the Puntarenas province. Flies (Diptera), including but not limited to the families Streblidae, Tabanidae, Tachinidae, and Heleomyzidae, were reported in caves. Parasitic wingless flies *Strebla wiedemanni* Kolenati, 1856 and *Trichobius parasiticus* Gervais, 1844 were collected from vampire bats in various parts of the country. A single record of Ephemeroptera was reported from the Corredores cave. Ants (Formicidae) were observed in at least nine caves. Other Hymenoptera included the families Eumenidae, Ichneumonidae,

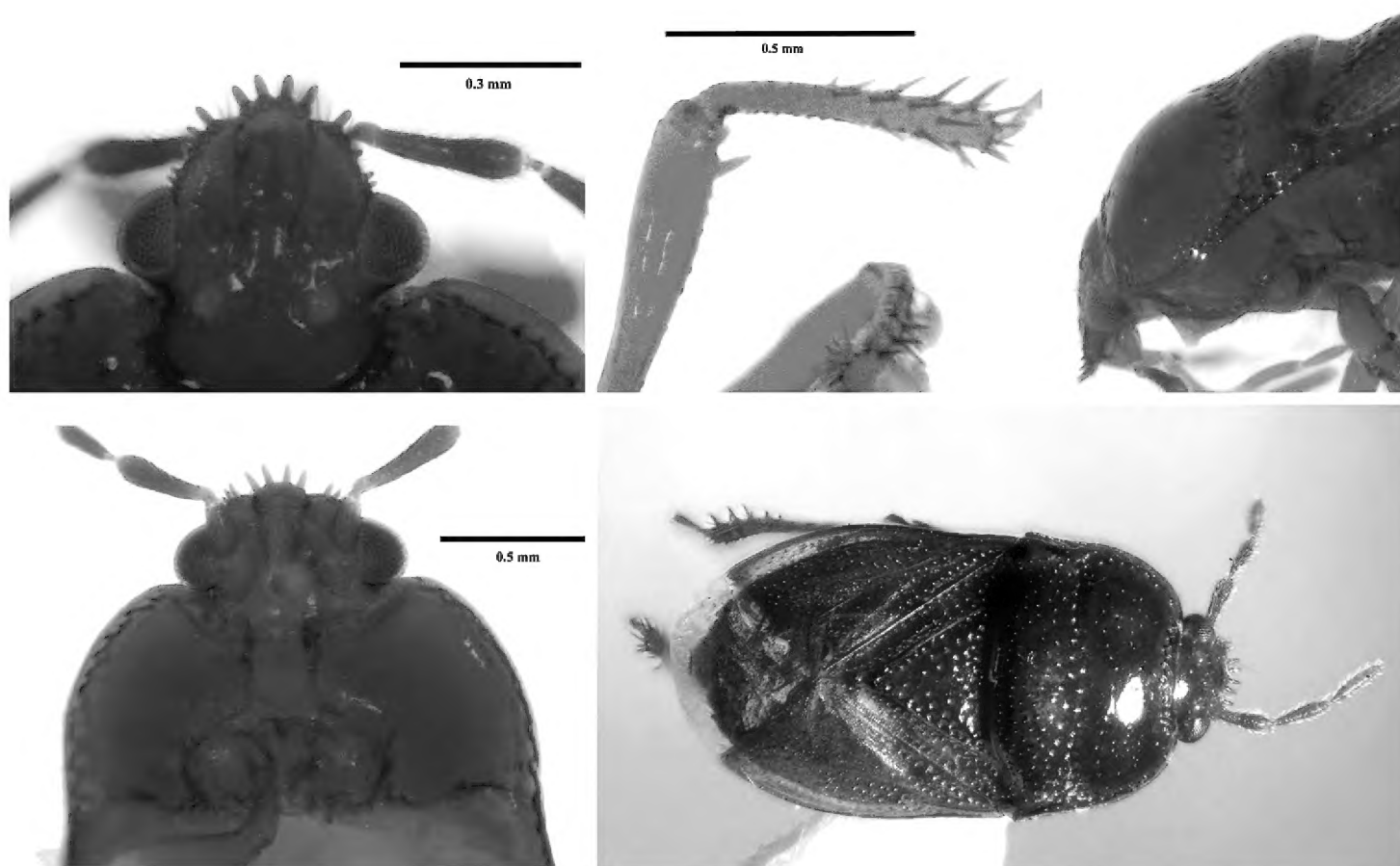


Figure 5. Morphological characteristics of the true bug (*Amnestus subferrugineus*) found in Costa Rican caves.

Taxon	CS	N	References
Isopoda			
Oniscidea		11	(Graening 2004; Hempel 1989; Lips and Lips 2008; Palacios 1994; Peacock and Hempel 1993; Strinati et al. 1987), ND
Armadillidae		1	ND
ARACHNIDA			
Opiliones			
Phalangodidae		4	(Peacock and Hempel 1993)
Zalmoxidae			
<i>Pachylicus hispidus</i> Goodnight & Goodnight, 1983		1	(Goodnight and Goodnight 1983; Juberthie and Strinati 1994)
<i>Panopiliops inops</i> Goodnight & Goodnight, 1983		1	(Goodnight and Goodnight 1983; Juberthie and Strinati 1994)
Indet.		9	(Graening 2004; Hempel 1989; Lips and Lips 2008; Peacock and Hempel 1993), ND
Acari			
Acariformes			
Pyemotidae		1	(Palacios 1994)
Ixodida		1	(Hempel 1989)
Mesostigmata			
Ascidae		1	(Palacios 1994)
Dinychidae			
<i>Urodiaspis</i> sp.		1	(Palacios 1994)
Macronyssidae			
<i>Radfordiella desmodi</i> Radovsky, 1967		1	(Rojas et al. 2008)
Spinturnicidae			
<i>Periglischrus herrenai</i> Machado-Allison, 1965		1	(Rojas et al. 2008)
Uropodidae			
<i>Neodiscopoma</i> sp.		1	(Palacios 1994)
Indet.		1	(Palacios 1994)
Oribatida			
Carabodidae		1	(Palacios 1994)
Galunmidae		1	(Lips and Lips 2008)
Indet.		1	(Lips and Lips 2008)
Trombidiformes			
Arrenuridae			
<i>Arrenurus golfensis</i> Cook, 1980		1	(Juberthie and Strinati 1994)
<i>Arrenurus plevamus</i> Cook, 1980		1	(Juberthie and Strinati 1994)
<i>Arrenurus zukovus</i> Cook, 1980		1	(Juberthie and Strinati 1994)
Hydrachnellae			
<i>Protolimnesia mesoamericana</i> Cook, 1980		1	(Juberthie and Strinati 1994)
Limnesiidae			
<i>Neomamersa costarriquensis</i> Cook, 1980		PS [§]	(Juberthie and Strinati 1994)
<i>Neomamersa decussa</i> Cook, 1980		PS [§]	(Juberthie and Strinati 1994)
<i>Psammolimnesia costarriquena</i> Cook, 1980		PS [§]	(Juberthie and Strinati 1994)
Omartacaridae			
<i>Omartacarus motasi</i> Cook, 1980		NC [§]	(Juberthie and Strinati 1994)
Rhagidiidae		1	(Palacios 1994)
Torrenticolidae			
<i>Torrenticola amala</i> Cook, 1980		1	(Juberthie and Strinati 1994)
<i>Frontipodopsis mesoamericana</i> Cook, 1980		1	(Juberthie and Strinati 1994)
<i>Frontipodopsis staheli</i> Walter, 1919		1	(Juberthie and Strinati 1994)
<i>Maharashtracarus neotropicus</i> Cook, 1980		1	(Juberthie and Strinati 1994)

Taxon	CS	N	References
Acari indet.		14	(Graening 2004; Hempel 1989; Lips and Lips 2008; Peacock and Hempel 1993; Strinati et al. 1987), ND
Pseudoscorpiones		5	(Lips and Lips 2008; Palacios 1994; Peacock and Hempel 1993; Strinati et al. 1987), ND
Scorpiones		3	(Hempel 1989; Peacock and Hempel 1993; Strinati et al. 1987)
Araneae			
Attidae		1	ND
Ctenidae			
<i>Ctenus</i> sp.		1	ND
<i>Ancylometes bogotensis</i> (Keyserling, 1877)		1	ND
Dysderidae		1	(Alpizar et al. 2006)
Lycosidae		1	ND
Segestriidae			
<i>Ariadna isthmica</i> Beatty, 1970		1	(Alpizar et al. 2006)
Theraphosidae		2	(Alpizar et al. 2006), ND
<i>Sericopelma upala</i> Valerio, 1980	LEY-RTP	1	(Alpizar et al. 2006)
Theridiidae		1	(Alpizar et al. 2006)
Theridiosomatidae		1	(Alpizar et al. 2006)
Trechaleidae			
<i>Trechalea</i> sp.		1	ND
Araneae indet.		20	(Graening 2004; Hapka et al. 1992; Hempel 1989; Lips and Lips 2008; Quesada and Deleva 2016; Palacios 1994; Peacock and Hempel 1993; Strinati et al. 1987)
Amblypygi			
Phrynidae			
<i>Paraphrynus laevifrons</i> (Pocock, 1894)		1	(Mullinex 1975; Juberthie and Strinati 1994; Alpizar et al. 2006)
<i>Paraphrynus viridiceps</i> (Pocock, 1894) [†]		7	(Peacock and Hempel 1993)
<i>Paraphrynus</i> sp.		7	ND
Phrynidae indet.		20	(Graening 2004; Debeljak 1988; Hapka et al. 1992; Hempel 1989; Lips and Lips 2008; Quesada 2018; Peacock and Hempel 1993; Strinati et al. 1987), ND
Schizomida		5	(Lips and Lips 2008; Juberthie and Strinati 1994; Strinati et al. 1987)
SYMPHYLA			
Symphyla indet.		2	(Lips and Lips 2008; Strinati et al. 1987)
CHILOPODA			
Chilopoda indet.		3	(Lips and Lips 2008; Strinati et al. 1987), ND
DIPLOPODA			
Polyxenidae		1	(Palacios 1994)
Diplopoda indet.		17	(Graening 2004; Hempel 1989; Lips and Lips 2008; Palacios 1994; Peacock and Hempel 1993; Strinati et al. 1987), ND
ENTOGNATHA			
COLLEMBOLA			
Neelipleona			
Neelidae			
<i>Megalothorax cf. minimus</i> Willem, 1900		1	(Palacios 1994)
<i>Megalothorax</i> sp.		1	(Palacios 1994)
Entomobryomorpha			
Paronellidae			
<i>Cyphodeus</i> sp.		1	(Juberthie and Strinati 1994)
<i>Trogolaphysa</i> sp.		1	(Palacios 1994)

Taxon	CS	N	References
Isotomidae			
<i>Folsomides</i> sp.		1	(Palacios 1994)
<i>Folsomina onychiurina</i> Denis, 1931		1	(Palacios 1994)
<i>Isotomurus minor</i> UN		1	(Palacios 1994)
<i>Isotomiella cf. minor</i> (Schäffer, 1896)		1	(Palacios 1994)
Collembola indet.		1	(Hapka et al. 1992; Quesada and Deleva 2016; Lips and Lips 2008; Peacock and Hempel 1993; Strinati et al. 1987), ND
Diplura			
Japygidae		1	(Strinati et al. 1987)
Diplura indet.		4	(Graening 2004; Hempel 1989; Lips and Lips 2008), ND
INSECTA			
Archaeognatha			
Meinertellidae			
<i>Grasiella</i> sp.		1	(Juberthie and Strinati 1994)
Zygentoma			
Nicoletiidae			
<i>Nicoletia cf. phytophile</i> Gervais, 1844		1	(Juberthie and Strinati 1994)
Zygentoma (reported as Thysanura)		1	(Strinati et al. 1987)
Ephemeroptera			
Heptageniidae		1	ND
Odonata		2	(Hempel 1989; Peacock and Hempel 1993)
Orthoptera			
Acrididae		1	(Hempel 1989)
Gryllacrididae		1	(Hempel 1989)
Gryllidae		1	(Hempel 1989)
Phalangopsidae		11	(Ulloa and Quesada 2010), ND
Tettigoniidae		1	(Hempel 1989)
Orthoptera indet.		12	(Quesada and Deleva 2016; Goicoechea 2010; Graening 2004; Hapka et al. 1992; Lips and Lips 2008; Peacock and Hempel 1993; Strinati et al. 1987)
Neuroptera			
Chrysopidae		1	(Hempel 1989)
Myrmeleontidae		2	(Graening 2004; Hempel 1989)
Dermaptera		7	(Lips and Lips 2008; Peacock and Hempel 1993)
Mantodea			
Mantidae		1	(Hempel 1989)
Blattodea			
Blaberidae			
<i>Blaberus giganteus</i> (Linnaeus, 1758)		3	(Graening 2004), ND
<i>Blaberus</i> sp.		1	(Ulloa and Quesada 2010)
Ectobiidae			
<i>Megaloblatta blaberoidea</i> (Walker, 1871) (as <i>M. rufipes</i> Dohrn, 1887)		1	(Palacios 1994)
Blattodea indet.		16	(Hapka et al. 1992; Hempel 1989; Lips and Lips 2008; Peacock and Hempel 1993), ND
Isoptera		1	(Hempel 1989)
Hemiptera			
Coreidae		1	(Hempel 1989)
Cicadellidae		1	(Hempel 1989)
Corixidae		1	(Hempel 1989)
Cydnidae			
<i>Amnestus subferrugineus</i> (Westwood, 1837)		1	ND

Taxon	CS	N	References
Fulgoridae		1	(Hempel 1989)
Lygaeidae		1	(Hempel 1989)
Pentatomidae		1	(Hapka et al. 1992; Hempel 1989)
Reduviidae			
<i>Triatoma</i> sp.		1	(Hempel 1989)
Hemiptera indet.		9	(Graening 2004; Hapka et al. 1992; Lips and Lips 2008; Peacock and Hempel 1993)
Hymenoptera			
Eumenidae		1	(Hempel 1989)
Formicidae		10	(Graening 2004; Hapka et al. 1992; Hempel 1989; Peacock and Hempel 1993), ND
Ichneumonidae		1	(Hempel 1989)
Mutillidae		1	(Graening 2004; Hempel 1989)
Pompilidae		1	(Hempel 1989)
Sphecidae		1	(Graening 2004)
Tenthredinidae		1	(Hempel 1989)
Vespidae		1	(Hempel 1989)
<i>Polistes instabilis</i> de Saussure, 1853		1	(Graening 2004)
Hymenoptera indet.		4	(Hempel 1989; Lips and Lips 2008; Peacock and Hempel 1993)
Coleoptera			
Alleculidae		1	(Hempel 1989)
Bostrichidae		1	(Hempel 1989)
Carabidae		2	(Graening 2004)
Cerambycidae		2	(Hempel 1989)
Cleridae		1	(Hempel 1989)
Curculionidae		1	(Hempel 1989)
Elateridae			
<i>Pyrophorus</i> sp.		1	(Hempel 1989)
Passalidae		1	(Hempel 1989)
Scarabaeidae		1	(Graening 2004)
Scolytidae		1	(Hempel 1989)
Staphylinidae		1	ND
Tenebrionidae		1	(Graening 2004)
<i>Zophobas atratus</i> (Fabricius, 1775)		2	(Tschinkel 1984; Juberthie and Strinati 1994)
Trogossitidae			
<i>Temnoscheila</i> (as <i>Temnochila</i>) sp.		1	(Hempel 1989)
Coleoptera indet.		12	(Hapka et al. 1992; Lips and Lips 2008; Palacios 1994; Peacock and Hempel 1993)
Trichoptera		1	(Hempel 1989)
Lepidoptera			
Nymphalidae (as Brassolidae)		1	(Hempel 1989)
Hesperiidae		1	(Hempel 1989)
Lycaenidae		1	(Hempel 1989)
Noctuidae		1	(Hempel 1989)
Nymphalidae		1	(Hempel 1989)
Tineidae		1	(Lips and Lips 2008)
Lepidoptera indet.		3	(Hapka et al. 1992; Lips and Lips 2008; Peacock and Hempel 1993, (Strinati et al. 1987)
Diptera			
Heleomyzidae		1	(Graening 2004)
Streblidae			
<i>Exastinion clovisi</i> (Pessoa & Guimarães, 1937)		1	(Mitchell et al. 2018)

Taxon	CS	N	References
<i>Megistopoda aranea</i> (Coquillett, 1899)		1	(Mitchell et al. 2018)
<i>Strebla wiedemanni</i> Kolenati, 1863		1	(Rojas et al. 2008)
<i>Trichobius lionycteridis</i> Wenzel, 1966		1	(Mitchell et al. 2018)
<i>Trichobius pallidus</i> (Curran, 1934)		3	(Mitchell et al. 2018)
<i>Trichobius parasiticus</i> Gervais, 1844		1	(Rojas et al. 2008)
Indet.		1	(Hempel 1989)
Tabanidae		1	(Hempel 1989)
Tachinidae		1	(Hempel 1989)
Insecta indet.		15	(Debeljak 1988; Goicoechea 2010a; Lips and Lips 2008), ND
Unknown arthropods		4	(Lips and Lips 2008)
Unknown invertebrates		5	(Lips and Lips 2008)

† - ND - new data: original contribution to this paper, ‡ - stygobiont, § - some sources report a region instead of a single site: PS – Puntarenas, NC – Nicoya, | - species is most likely misidentified.

Entognatha

Springtails (Collembola) have also been observed in Costa Rican caves, but there have only been a few mentions of lower taxa. *Megalothorax minimus* Willem, 1900, *Isotomiella minor* (Schaeffer, 1896), *Folsomina onychiurina* (Denis, 1931), *Folsomides* sp., *Isotomurus* sp. Bristletails (Diplura) were found in caves, but no specific information regarding their taxonomy was available.

Other invertebrates

Reports exist regarding worms belonging to Turbellaria, Oligochaeta, and Clitellata. The term “worm” was also used as a general morphological descriptor for invertebrates observed within caves.

Vertebrates

Actinopterygii

Two species of Costa Rican fish (Actinopterygii) display adaptations to cave life. These species are the three-barbed catfish from the *Rhamdia* genus and the characid Mexican tetra (*Psalidodon fasciatus* (De Filippi, 1853)). Pale-colored individuals of the catfish species *Rhamdia guatemalensis* (Günther, 1864) were observed in the Corredores and Bananal cave systems as well as in other adjacent caves (Fig. 6). Furthermore, pale-colored individuals of the same genus have been reported in an artificial tunnel near Arenal volcano. The Mexican tetra, also known as the blind cave fish, was studied in a karstic spring in Guanacaste. Livebearing fishes from the *Brachyrhaphis* genus, rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), Nile tilapia (*Oreochromis niloticus* (Linnaeus, 1758)), and various unidentified characids (Characidae), cyprinids (Cyprinidae), and catfish (Hep-
tapteridae) were reported from caves and springs (Table 2, Suppl. material 1).



Figure 6. Pale-colored catfish (*Rhamdia guatemalensis*) in Corredores cave.

Amphibia

Frogs and toads (Anura) were observed both at the entrances and deep inside the caves (Fig. 7). We found records of at least eight species belonging to five frog and toad families (Table 2). These included poison dart frogs, *Dendrobates auratus* (Girard, 1855), *Oophaga granulifera* (Taylor, 1958), thin-toed frogs (*Leptodactylus savagei* Heyer, 2005), grass frogs (*Lithobates forreri* (Boulenger, 1883)), *L. warszewitschii* (Schmidt, 1857)), toads (*Rhinella horribilis* (Wiegmann, 1833)), and *Incilius aucoinae* (O'Neill & Mendelson, 2004). Cane toads (*Rhinella horribilis*) were observed at the bottom vertical shafts on several occasions. There were two observations of tadpoles from the Carma and Corredores caves. The cave “Pozo Sapo Gordo” (“Fat Toad Abyss”) received its name because of the presence of a large cane toad.

Reptilia

The South American snapping turtle (*Chelydra acutirostris* (Peters, 1862)) and the white-lipped mud turtle (*Kinosternon leucostomum* (Duméril, Bibron & Duméril, 1851)) were observed on multiple occasions deep inside a flooded artificial tunnel (Fig. 8A, B). The fer-de-lance (*Bothrops asper* (Garman, 1883)) was observed both at the entrances and in narrow passages inside the caves (Fig. 8C). The caves “Serpiente Dormida,” “Pozo del Chispero,” “Terciopelo,” and “Pozo Oropel” were named after encounters between snakes and cave explorers. The aquatic prawn snake (*Hydromorphus concolor* (Peters, 1859)) was observed in an artificial tunnel near Arenal volcano

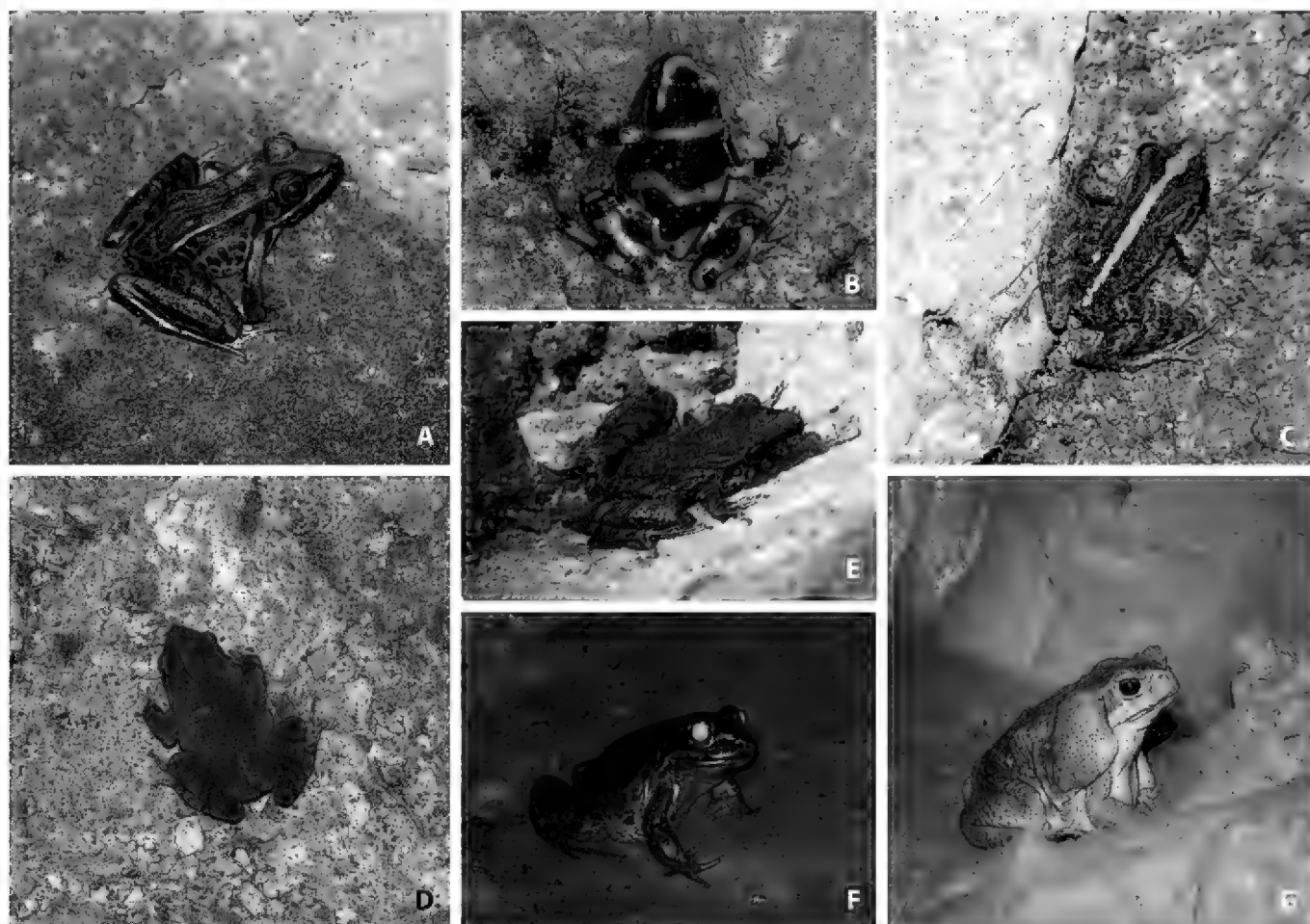


Figure 7. Frogs and toads found in Costa Rican caves **A** forrers grass frog (*Lithobates forreri*) **B** green and black poison dart frog (*Dendrobates auratus*) **C, E** Fitzinger's Robber Frog (*Craugastor fitzingeri*) **D** rain-forest toad (*Incilius aucoinae*) **F** thin-toed frog (*Leptodactylus savagei*) **G** cane toad (*Rhinella horribilis*).

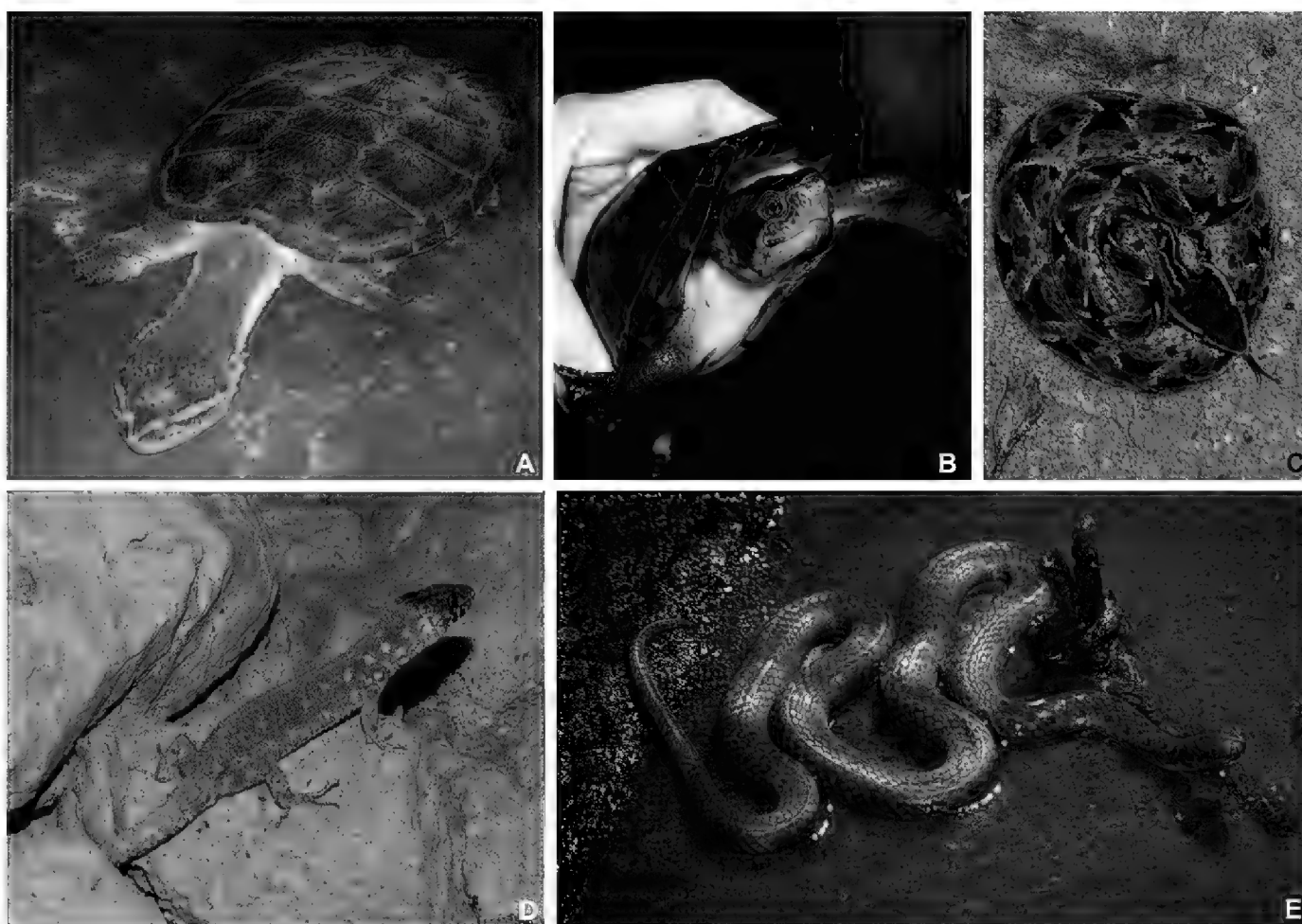


Figure 8. Reptiles living in caves **A** South American snapping turtle (*Chelydra acutirostris*) **B** white-lipped mud turtle (*Kinosternon leucostomum*) **C** fer-de-lance - (*Bothrops asper*) **D** Costa Rican tropical night lizard (*Lepidophyma reticulatum*) **E** prawn snake (*Hydromorphus concolor*).

(Fig. 8E). Additionally, there were sightings of a boa (Boaidae) and an unknown species of snake, solely identified based on visual characteristics. The night lizard (*Lepidophyma reticulatum* (Taylor, 1955)) was observed in at least three caves (Fig. 8D). Reports also mentioned the presence of geckos (Geckota) within a cave.

Birds

Information regarding birds residing in and around caves was limited. However, there were a few noteworthy observations. The entrance of an artificial tunnel near Rio Ter-raba served as a nesting site for a black vulture (*Coragyps atratus* (Bechstein, 1793)). Additionally, sightings near cave entrances included a great tinamou (*Tinamus major* (Gmelin, 1789)) and a wood rail (*Aramides cajaneus* Müller, 1776).

Mammalia

Non-volant mammals in the subterranean ecosystem predominantly comprise of small predators and rodents. Various tracks attributed to carnivorous mammals such as cats and mustelids have been observed in different caves. In Palo Verde National Park, the “Tigre cave” presumably served as a roosting site for a large cat, possibly a jaguar or puma. An ocelot (*Leopardus pardalis* (Linnaeus, 1758)) was sighted in an artificial tunnel, and bones of kinkajou (*Potos flavus* (Schreber, 1774)) were discovered in Trampa vertical cave. Opossums (Didelphidae) of at least four species were observed within the caves. Caves in Barra Honda yielded bones from various mammals, including pec-cary (*Dicotyles tajacu* (Linnaeus, 1758)), cottontail rabbit (*Sylvilagus* sp.), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), armadillo (*Dasypus novemcinctus* (Linnaeus, 1758)), porcupine (*Coendou mexicanus*), and several species of rodents (Ro-dentia). It remains unclear whether these mammals entered the caves or whether their carcasses were brought in by predators.

Table 2. Classes of vertebrates in Costa Rican caves. The first column represents the taxon. The second column (CS) presents the conservation status of the species: 1. IUCN Red List - “Least Concern” (LC), “Not Evaluated” (NE), “Data Deficient” DD), “Vulnerable” VU), 2. Included in the CITES convention: CITES, 3. Included in the annexes of the Costa Rican Biodiversity law (LEY) – “Vulnerable” (VU), and “Reduced or threatened population” (TR). The third column (N) represents the number of individual sites where the taxon was present. The last column presents the sources of information regarding the taxa.

Taxon	CS	N	Reference(s)
ACTINOPTERYGII			
Cypriniformes			
Cyprinidae		1	(Peacock and Hempel 1993)
Characiformes			
Characidae			
<i>Psalidodon fasciatus</i> (De Filippi, 1853) (as <i>Astyanax fasciatus</i>) [§]	IUCN-LC	1	(Romero 1985)
Characidae indet.		1	ND

Taxon	CS	N	Reference(s)
Siluriformes			
Heptapteridae			
<i>Rhamdia guatemalensis</i> (Günther, 1864) [§]	IUCN-LC	5	(Debeljak 1988; Juberthie and Strinati 1994; Grupo Espeleológico Anthros 2023), ND
<i>Rhamdia nicaraguensis</i> (Günther, 1864)	IUCN-LC	1	(Gonzalez 2012)
<i>Rhamdia</i> sp.		4	(Strinati et al. 1987), ND
Heptapteridae indet.		3	(Quesada and Deleva 2016; Peacock and Hempel 1993)
Salmoniformes			
Salmonidae			
<i>Oncorhynchus mykiss</i> (Walbaum, 1792)		1	(González 2010)
Cichliformes			
Cichlidae			
<i>Oreochromis niloticus</i> (Linnaeus, 1758)	IUCN-LC	1	(Gonzalez 2012)
Cyprinodontiformes			
Poeciliidae			
<i>Brachyrhaphis rhabdophora</i> (Regan, 1908)	IUCN-VU	1	(Romero 1985)
<i>Brachyrhaphis olomina</i> (Meek, 1914)	IUCN-DD	1	(Gonzalez 2012)
Actinopterygii indet. [‡]		1	(Woodman 1988)
AMPHIBIA			
Anura			
Craugastoridae			
<i>Craugastor fitzingeri</i> (Schmidt, 1857)	IUCN-LC	2	(Quesada 2018), ND
Bufonidae			
<i>Rhinella horribilis</i> (Wiegmann, 1833)	IUCN-LC	5	(Gonzalez 2012; Graening 2004), ND
<i>Incilius aucoinae</i> (O'Neill & Mendelson, 2004)	IUCN-LC	1	ND
Bufonidae indet.		2	(Hapka et al. 1992), ND
Dendrobatidae			
<i>Dendrobates auratus</i> (Girard, 1855)	IUCN-LC, CITES-II, LEY-RTP	1	(Quesada 2018), ND
<i>Oophaga granulifera</i> (Taylor, 1958)	IUCN-VU, CITES-II, LEY-RTP	1	ND
Leptodactylidae			
<i>Leptodactylus savagei</i> Heyer, 2005	IUCN-LC	2	(Quesada and Deleva 2016), ND
Ranidae			
<i>Lithobates warszewitschii</i> (Schmidt, 1857)	IUCN-LC	1	(Ulloa and Quesada 2010)
<i>Lithobates forreri</i> (Boulenger, 1883)	IUCN-LC	1	ND
Ranidae indet.		1	(Lips and Lips 2008; Peacock and Hempel 1993; Strinati et al. 1987), ND
Anura indet.		1	(Quesada 2009b)
Amphibia indet. [‡]		8	(Woodman 1988)
REPTILIA			
Testudines			
Chelydridae			
<i>Chelydra acutirostris</i> Peters, 1862	CITES-II	1	(Gonzalez 2012), ND
Kinosternidae			
<i>Kinosternon leucostomum</i> (Duméril, Bibron & Duméril, 1851)	CITES-II	1	(Gonzalez 2012), ND
Squamata			
Boaidae		2	(Lyon et al. 2004), Vicente-Santos 2019)

Taxon	CS	N	Reference(s)
Colubridae			
<i>Hydromorphus concolor</i> Peters, 1859	IUCN-LC	1	ND
Viperidae			
<i>Bothrops asper</i> (Garman, 1883)	IUCN-LC	2	(Quesada 2009a), ND
<i>Bothriechis schlegelii</i> (Berthold, 1846)	IUCN-LC	1	(Hapka et al. 1992)
Serpentes indet.		2	(Hapka et al. 1992)
Xantusiidae			
<i>Lepidophyma reticulatum</i> Taylor, 1955	IUCN-LC	2	(Ulloa 2009b), ND
Gekkota		1	(Graening 2004)
Reptilia indet. [‡]		1	(Goicoechea 2010; Graening 2004; Hapka et al. 1992; Woodman 1988)
AVES			
Tinamiformes			
Tinamidae			
<i>Tinamus major</i> (Gmelin, 1789)	IUCN-LC	1	ND
Gruiformes			
Rallidae			
<i>Aramides cajaneus</i> (Müller, 1776)	IUCN-LC	1	(Gonzalez 2012)
Cathartiformes			
Cathartidae			
<i>Coragyps atratus</i> (Bechstein, 1793)	IUCN-LC	1	(Quesada 2018), ND
MAMMALIA			
Cingulata			
Dasypodidae			
<i>Dasypus novemcinctus</i> Linnaeus, 1758 [‡]	IUCN-LC	2	(Hempel 1989; Woodman 1988)
Didelphimorphia			
Didelphidae			
<i>Caluromys derbianus</i> (Waterhouse, 1841)	IUCN-LC	1	(Trescott and Vicente-Santos 2019)
<i>Didelphis marsupialis</i> Linnaeus, 1758	IUCN-LC	1	(Hempel 1989)
<i>Didelphis</i> sp. [‡]		1	(Woodman 1988)
<i>Marmosa mexicana</i> Merriam, 1897	IUCN-LC	1	(Hempel 1989)
<i>Philander opossum</i> (Linnaeus, 1758)	IUCN-LC	1	(Gonzalez 2012)
Didelphidae indet.		2	ND
Lagomorpha			
Leporidae			
<i>Sylvilagus</i> sp.		2	(Hempel 1989)
Rodentia			
Cricetidae			
<i>Oryzomys</i> sp.		1	(Hempel 1989)
<i>Ototylomys phyllotis</i> Merriam, 1901 [‡]	IUCN-LC	1	(Hempel 1989; Woodman 1988)
<i>Peromyscus stirtoni</i> Dickey, 1928 [‡]	IUCN-LC	1	(Woodman 1988)
<i>Peromyscus</i> sp. [‡]		1	(Woodman 1988)
<i>Reithrodontomys</i> sp. [‡]		1	(Woodman 1988)
<i>Sigmodon hispidus</i> Say & Ord, 1825 [‡]	IUCN-LC	3	(Hempel 1989; Woodman 1988)
Cuniculidae			
<i>Cuniculus paca</i> (Linnaeus, 1766)	IUCN-LC, LEY-RTP	3	(Hempel 1989; Woodman 1988)
Dasyproctidae			
<i>Dasyprocta punctata</i> (Gray, 1842) [‡]	IUCN-LC	4	(Hempel 1989; Lips and Lips 2008; Woodman 1988)
Erethizontidae			
<i>Coendou mexicanus</i> (Kerr, 1792) [‡]	IUCN-LC	2	(Hempel 1989; Woodman 1988)
Geomyidae			
<i>Orthogeomys</i> sp.		1	(Hempel 1989)

Taxon	CS	N	Reference(s)
Heteromyidae			
<i>Liomys salvini</i> (Thomas, 1893) [‡]	IUCN-LC, LEY-RTP	2	(Hempel 1989; Woodman 1988)
Carnivora			
Procyonidae			
<i>Potos flavus</i> (Schreber, 1774) [‡]	IUCN-LC	1	(Hempel 1989)
Felidae			
<i>Leopardus pardalis</i> (Linnaeus, 1758)	IUCN-LC, CITES-I, LEY-VU	1	(Gonzalez 2012)
Felidae indet.		2	(Graening 2004; Hapka et al. 1992)
Carnivora indet.		1	ND
Perissodactyla			
Equidae			
<i>Equus ferus caballus</i> Linnaeus, 1758 [‡]		1	ND
Artiodactyla			
Cervidae			
<i>Odocoileus virginianus</i> (Zimmermann, 1780) [‡]	IUCN-LC	1	(Hempel 1989)
Tayassuidae			
<i>Dicotyles tajacu</i> (Linnaeus, 1758) [‡]	IUCN-LC	2	(Hempel 1989; Woodman 1988)

† - ND - new data: original contribution to this paper, ‡ - bones, § - observed individuals with morphological adaptations toward cave life.

Chiroptera

Bats were documented at least in 97 subterranean sites throughout the country (Table 3). Thirty-six bat species from the families Emballonuridae, Mormoopidae, Natalidae, Noctilionidae, Phyllostomidae, and Vespertilionidae have been reported inside caves or at their entrances (Fig. 9). The most frequently observed species was Seba’s short-tailed bat (*Carollia perspicillata* (Linnaeus, 1758)), found in 44 locations, followed by the common vampire bat (*Desmodus rotundus* (Geoffroy, 1810)) (34 locations), greater dog-like bat (*Peropteryx kappleri* (Peters, 1867)) (22 locations), greater sac-winged bat (*Saccopteryx bilineata* (Temminck, 1838)) (17 locations), Pallas’s long-tongued bat (*Glossophaga soricina* (Pallas, 1766)) (12 locations), and Tomes’ sword-nosed bat (*Lonchorhina aurita* Tomes, 1863 (10 locations)). Parnell’s mustached bat was reported as either *Pteronotus parnellii* or *P. mesoamericanus* at 17 locations. The funnel-eared bat, found in 10 locations, was identified as *Natalus mexicanus* in some sources and either *Natalus stramineus* or *Natalus lanatus* in others. However, these scientific names are currently accepted as synonyms, suggesting that they likely represent the same species (Solari 2019). Regarding the importance of caves as bat roosts, eight species (*Glossophaga leachii*, *Lonchophylla robusta*, *Lonchorhina aurita*, *Natalus mexicanus*, *Pteronotus davyi*, *Pteronotus gymnonotus*, *Pteronotus mesoamericanus*, and *Pteronotus personatus*) were considered cave-dependant. Among the caves with the highest reported bat species richness were La Trampa (13 species), Corredores (11 species), Gabinarraca (8 species), Emus (8 species), Damas (7 species) Pozo Hediondo (6 species), and an artificial tunnel near Arenal volcano (6 species) (Suppl. material 1). The global conservation status of all the observed cave-dwelling bats was Least Concern. The Costa Rican Law for the protection of wildlife included four species (*Anoura cultrata*, *Chrotopterus auritus*, *Lonchophylla concava* and *Trinycteris nicefori*) in the category “Reduced or Threatened population” (Table 3).

Table 3. Bats (Chiroptera) in Costa Rican caves. The first column represents the taxon. The second column (CD) represents the species dependence on caves. The third column (CS) shows the species conservation status, according to the IUCN Red List (IUCN) and the Costa Rican Biodiversity law (LEY). The abbreviations are “Least concern” (LC) and “reduced or threatened population” (RTP). The fourth column (№) represents the number of individual sites where the taxon was present. The last column presents the sources of information regarding the taxa.

Taxon	CD	CS	№	References
Emballonuridae				
<i>Balantiopteryx plicata</i> (Peters, 1867)		IUCN-LC	2	(Timm and McClearn 2007; Graening 2004)
<i>Peropteryx kappleri</i> (Peters, 1867)		IUCN-LC	22	(Deleva and Chaverri 2018; Goicoechea and Quesada 2019; Lips and Lips 2008; Quesada 2009b), ND [†]
<i>Peropteryx macrotis</i> (Wagner, 1843)		IUCN-LC	2	(Deleva and Chaverri 2018)
<i>Peropteryx</i> sp.		IUCN-LC	1	(Lips and Lips 2008),
<i>Saccopteryx bilineata</i> (Temminck, 1838)		IUCN-LC	17	(Deleva and Chaverri 2018; Goicoechea and Quesada 2019; Gonzalez 2012; Quesada 2018; Quesada and Deleva 2016; Timm and McClearn 2007)
Mormoopidae				
<i>Pteronotus davyi</i> (Gray, 1838)	+	IUCN-LC	4	(Cubero and Artavia 2016; Flemming 2003; Hempel 1989)
<i>Pteronotus gymnonotus</i> (Natterer, 1843)	+	IUCN-LC	5	(Cubero and Artavia 2016; Deleva and Chaverri 2018), ND
<i>Pteronotus parnellii</i> (= <i>mesoamericanus</i>) (Gray, 1843)	+	IUCN-LC	17	(Cubero and Artavia 2016; Deleva and Chaverri 2018; Gonzalez 2012; Heithaus and Fleming 1978; Hempel 1989; Mitchell et al. 2018; Quesada 2018; Quesada and Deleva 2016; Trescott and Vicente-Santos 2019), ND
<i>Pteronotus personatus</i> (Wagner, 1843)	+	IUCN-LC	3	(Cubero and Artavia 2016), Deleva and Chaverri 2018; Lips and Lips 2008)
<i>Pteronotus</i> sp.			2	(Hempel 1989; Ulloa and Quesada 2010), ND
Natalidae				
<i>Natalus mexicanus</i> (= <i>lanatus</i> or <i>stramineus</i>) (Wagner, 1843)	+	IUCN-LC	10	(Cubero and Artavia 2016; Deleva and Chaverri 2018; Hempel 1989; Flemming 2003; Rodríguez-Herrera et al. 2011; Trescott and Vicente-Santos 2019), ND
Noctilionidae				
<i>Noctilio leporinus</i> (Linnaeus, 1758)		IUCN-LC	1	(Romero 1985)
Phyllostomidae				
<i>Anoura cultrata</i> Handley, 1960		IUCN-LC, LEY-RTP	1	(Mitchell et al. 2018)
<i>Anoura</i> sp.			2	(Deleva and Chaverri 2018)
<i>Artibeus jamaicensis</i> Leach, 1821		IUCN-LC	10	(Cubero and Artavia 2016; Deleva and Chaverri 2018; Goicoechea and Quesada 2019; Hempel 1989; Mitchell et al. 2018; Quesada 2018), ND
<i>Artibeus lituratus</i> (Olfers, 1818)		IUCN-LC	1	(Cubero and Artavia 2016)
<i>Artibeus</i> sp.			3	(Hempel 1989)
<i>Carollia perspicillata</i> (Linnaeus, 1758)		IUCN-LC	44	(Cubero and Artavia 2016; Deleva and Chaverri 2018; Fleming and Heithaus 1986; Flemming 2003; Gonzalez 2012; Goicoechea and Quesada 2019; Heithaus and Fleming 1978; Hempel 1989; Lips and Lips 2008; Mitchell et al. 2018; Ulloa 2009b; Quesada and Deleva 2016; Quesada 2018; Trescott and Vicente-Santos 2019; Villalobos-Chaves et al. 2016), ND
<i>Carollia sowelli</i> Baker, Solari & Hoffmann, 2002		IUCN-LC	2	(Deleva and Chaverri 2018; Villalobos-Chaves et al. 2016)
<i>Carollia subrufa</i> (Hahn, 1905)		IUCN-LC	1	(Heithaus and Fleming 1978)
<i>Chrotopterus auritus</i> Peters, 1856	+	IUCN-LC, LEY-RTP	2	(Deleva and Chaverri 2018; Graening 2004)

Taxon	CD	CS	Nº	References
<i>Dermanura phaeotis</i> Miller, 1902		IUCN-LC	1	(Cubero and Artavia 2016)
<i>Desmodus rotundus</i> (Geoffroy, 1810)		IUCN-LC	34	(Cubero and Artavia 2016; Deleva and Chaverri 2018; Gonzalez 2012; Goicoechea and Quesada 2019; Graening 2004; Hapka et al. 1992; Heithaus and Fleming 1978; Hempel 1989; Lips and Lips 2008; Peacock and Hempel 1993; Quesada 2013; Quesada 2015; Quesada and Deleva 2016; Trescott and Vicente-Santos 2019; Timm and McClearn 2007; Ulloa 2009b; Villalobos-Chaves et al. 2016; Vicente-Santos 2019), ND
<i>Diphylla ecaudata</i> Spix, 1823		IUCN-LC	4	(Cubero and Artavia 2016; Hempel 1989; Trescott and Vicente-Santos 2019), ND
<i>Glossophaga commissarisi</i> Gardner, 1962		IUCN-LC	1	(Cubero and Artavia 2016)
<i>Glossophaga leachii</i> Gray, 1844	+	IUCN-LC	1	(Cubero and Artavia 2016)
<i>Glossophaga soricina</i> (Pallas, 1766)		IUCN-LC	12	(Cubero and Artavia 2016; Deleva and Chaverri 2018; Gonzalez 2012; Flemming 2003; Hempel 1989; Lips and Lips 2008), ND
<i>Lamproncycteris brachyotis</i> (Dobson, 1879)		IUCN-LC	3	(Cubero and Artavia 2016)
<i>Lonchophylla concava</i> Goldman, 1914		IUCN-LC, LEY-RTP	3	(Deleva and Chaverri 2018)
<i>Lonchophylla robusta</i> Miller, 1912	+	IUCN-LC	7	(Armstrong 1969; Deleva and Chaverri 2018; Goicoechea and Quesada 2019; Lips and Lips 2008; Trescott and Vicente-Santos 2019), ND
<i>Lonchorhina aurita</i> Tomes, 1863	+	IUCN-LC	10	(Deleva and Chaverri 2018; Mitchell et al. 2018; Nelson 1965; Trescott and Deleva 2016; Trescott and Vicente-Santos 2019; Villalobos-Chaves et al. 2016; Vicente-Santos 2019), ND
<i>Micronycteris megalotis</i> (Gray, 1842)		IUCN-LC	2	(Hempel 1989; Peacock and Hempel 1993)
<i>Micronycteris microtis</i> (Miller, 1898)		IUCN-LC	1	(Villalobos-Chaves et al. 2016)
<i>Micronycteris schmidtorum</i> Sanborn, 1935		IUCN-LC	1	(Woodman 1988)
<i>Phyllostomus discolor</i> Wagner, 1843		IUCN-LC	1	(Deleva and Chaverri 2018)
<i>Phyllostomus hastatus</i> (Pallas, 1767)		IUCN-LC	6	(Deleva and Chaverri 2018; Goicoechea and Quesada 2019; Gonzalez 2012; Hempel 1989; Quesada and Deleva 2016; Timm and McClearn 2007), ND
<i>Phyllostomus</i> sp.			1	(Peacock and Hempel 1993)
<i>Tonatia saurophila</i> Koopman & Williams, 1951		IUCN-LC	1	(Trescott and Vicente-Santos 2019)
<i>Trachops cirrhosus</i> (Spix, 1823)		IUCN-LC	5	(Deleva and Chaverri 2018; Trescott and Vicente-Santos 2019; Vicente-Santos 2019), ND
<i>Trinycteris nicefori</i> Sanborn, 1949		IUCN-LC, LEY-RTP	2	(Vásquez and Artavia 2017)
Phyllostomidae indet.			10	(Aguilar 2010; Brizuela et al. 2015; Goicoechea 2019; Lips and Lips 2008; Madrigal 2010; Quesada and Alfaro 2005; Quesada 2015; Quesada and Deleva 2016), ND
Vespertilionidae				
<i>Rhogessa bickhami</i> Baird, Marchán-Rivadeneira, Pérez & Baker, 2012		IUCN-LC	1	(Cubero and Artavia 2016)
Chiroptera indet.			16	(Carvajal 2014; Hapka et al. 1992; Goicoechea 2018; Hempel 1989; Lips and Lips 2008; Peacock and Hempel 1993; Quesada 2010; Strinati et al. 1987; Trescott 2012; Ulloa 2012; Woodman 1988)

† - ND - new data: original contribution to this paper,

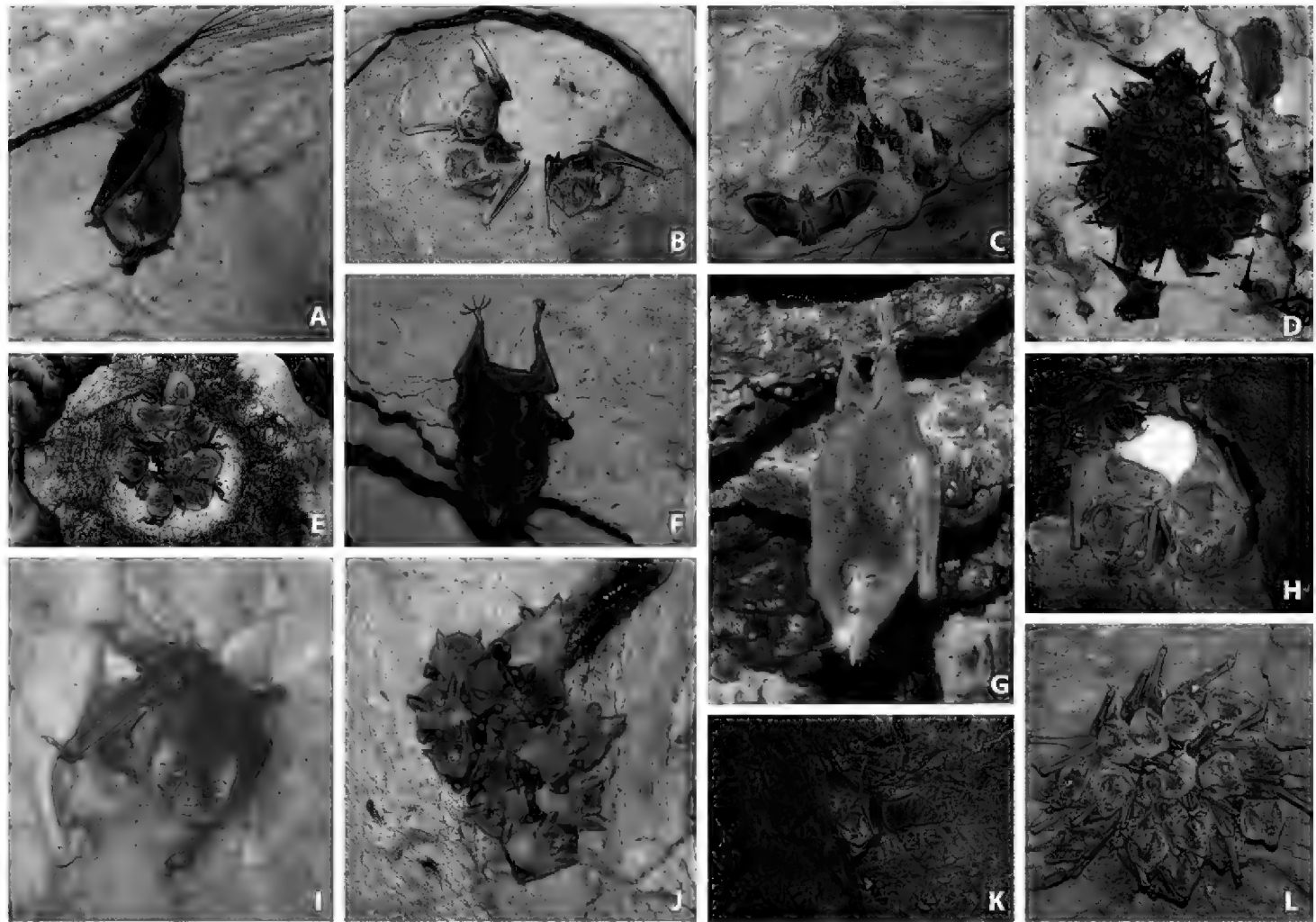


Figure 9. Cave-dwelling bats in Costa Rica **A** Mexican greater funnel-eared bat (*Natalus mexicanus*) **B** a group of common vampire bats (*Desmodus rotundus*) with pups **C** sword-nosed bats (*Lonchorhina aurita*) **D** Parnell's mustached bats (*Pteronotus parnellii*) **E** Jamaican fruit bat (*Artibeus jamaicensis*) **F** greater sac-winged bat (*Saccopteryx bilineata*) **G** Goldman's nectar bat (*Lonchophylla concava*) **H** a group of Seba's short-tailed bats (*Carollia perspicillata*) with an albino pup **I** hairy-legged vampire bat (*Diphylla ecaudata*) with a pup **J** orange nectar bat (*Lonchophylla robusta*) **K** fringe-lipped bat (*Trachops cirrhosus*) **L** greater spear-nosed bat (*Phyllostomus hastatus*).

Discussion

Our literature review and field observations of cave-dwelling fauna in Costa Rica yielded a database of 959 records encompassing 123 species, with the remainder mentioning higher taxonomic levels. Some literature records are expedition reports that introduce the possibility of misidentification, particularly in cases involving closely related species. However, the information gathered undoubtedly represents a valuable depiction of the current state of knowledge regarding cave-dwelling fauna in Costa Rica. There are a few noteworthy records of possible “trogllobites,” which are typical cave-dwelling organisms morphologically adapted to subterranean life. Notably, a freshwater crab from Southern Costa Rica, *Pseudothelphusa puntarenas*, has been described as a cave dweller (Hobbs, 1994). Furthermore, various specimens of springtails (*Trogolaphysa* sp.) and mites (Rhagidiidae) from Barra Honda (Palacios 1994) exhibit morphological adaptations that are indicative of cave life. Similarly, a single harvestman species from Southern Costa Rica (Goodnight and Goodnight 1983) displayed morphological changes that were attributed to cave adaptation.

Although only long-term studies could confirm their exact categorization, it is likely that most vertebrates in Costa Rican subterranean ecosystems fall under the category of troglophiles, referring to species that find suitable living conditions within caves but still rely on surface access for activities, such as feeding or reproduction. During our field observations, we frequently encountered cave-dwelling cane toads (*Rhinella horribilis*) thriving on abundant invertebrate prey as well as numerous frog species located near the entrances. A thin-toed frog (*Leptodactylus savagei*) was also noted in the caves. However, these species cannot be considered as true cave dwellers if they are unable to reproduce underground. Nonetheless, live tadpoles have been documented in subterranean lakes in Southern Costa Rica (Peacock and Hempel 1993), suggesting the potential for the long-term survival of cave-dwelling populations of amphibians. We confirm the recent commentary of Sperandei et al. (2023) that neotropical frogs should not be considered accidentals in caves and that more attention should be given to their monitoring in subterranean habitats. Reptiles such as night lizards (*Lepidophyma reticulatum*) and turtles (*Chelydra acutirostris*) inhabit deep subterranean passages. Additionally, two distinct fish species, the three-barbed catfish *Rhamdia guatemalensis* and the Mexican tetra *Psalidodon fasciatus*, exhibited signs of adaptation to subterranean life, such as pale coloration and reduced eye size (Romero 1985; Juberthie and Strinati 1994). Their biology, adaptations, and taxonomy have yet to be studied in detail.

Our study highlights that the number of taxa recorded in Costa Rican caves is relatively low compared to the country's enormous potential as a biodiversity hotspot (Avalos 2019). We argue that this is due to the lack of detailed research and low sampling effort rather than the true scarcity of biodiversity. It is also important to note that some subterranean sites in Costa Rica have not been studied and most have limited biospeleological records. For comparison purposes, the cave fauna of Venezuela, which has received considerable research attention, includes over 350 identified invertebrate species, 46 of which are classified as troglobites (Galán and Herrera 2006). A detailed review of Central American subterranean aquatic fauna revealed rich biodiversity in a relatively small geographic area (Reddell 1981; Mejía-Ortíz et al. 2021). Recent studies on a limited number of caves in Belize (Wynne and Pleytez 2005; Taylor et al. 2011) have resulted in the discovery of at least 80 unique taxa with possible new species for science. Several studies have focused on the diversity and ecology of cave invertebrates in the Guatemala (Pacheco et al. 2020; Pacheco et al. 2021). These studies are encouraging and could hint at the results expected in the Costa Rican caves if we apply a more systematic approach to biospeleological research.

Costa Rican caves and artificial subterranean sites are crucial habitats for bats, as most of them (72%, n=97) were occupied by these mammals. The existing literature shows that at least 52 bat species that occur in Costa Rica dwell in caves across their geographic ranges (Sagot and Chaverri 2015; Oliveira et al. 2018; IUCN 2023a). For example, studies conducted in Brazil have identified 81 species that inhabit caves (Oliveira et al. 2018; Barros and Bernard 2023). For Costa Rica, the studies we found focused primarily on quantifying the diversity of cave-dwelling bats, yet there is limited information on the abundance and the seasonal dynamics of populations (Peacock and Hempel 1993; Gonzalez 2012; Cubero and Artavia 2016; Villalobos-Chaves et al. 2016; Deleva

and Chaverri 2018). Since some species of bats that rely on caves as their roosting sites are highly specialized and may be more vulnerable to disturbance, it is crucial to identify and prioritize the conservation of important underground bat roosts in the country (Sagot and Chaverri 2015; Tanalgo et al. 2022). Long-term monitoring of cave-dwelling bats should be a high priority for local authorities, as it would provide a valuable contribution to research and conservation efforts in the country and decision-making for sustainable activities within caves, most notably tourism (Deleva and Chaverri 2018). Other research questions worth pursuing in future studies on Costa Rican bats are related to their ecology and behavior. Special attention must be paid to the importance of artificial subterranean sites such as roosts, as they can provide excellent conditions for bats and other animals (Gonzalez 2012; Deleva and Chaverri 2018). However, these are often overlooked in monitoring and conservation measures (Weigand et al. 2022; Deleva et al. 2023).

The relatively low number of species discovered in caves suggests the need to expand research on the subterranean fauna of Costa Rica. For example, there are considerable gaps in fundamental knowledge about whole taxonomic groups, such as Amphipoda, Schizomida, Gastropoda, and Diplura, and there are no studies on the ecology or behavior of cave organisms. A promising research topic would be to study in detail the adaptations of pale catfish toward cave life (Perdices et al. 2002) and more studies on the stygofauna. With the use of more advanced methods, such as environmental DNA (Saccò et al. 2022), acoustic monitoring, different trapping techniques, and citizen science, we believe that there is enormous potential for discovering new species and gaining a better understanding of the ecology and diversity of Costa Rica's subterranean ecosystems. In particular, we suggest that future studies focus on long-term investigations of cave invertebrate communities and compare them with other habitats in the country (Smith et al. 2023). Future studies should also include soil-dwelling organisms, particularly the Mesovoid Shallow Substratum (MSS). The study of MSS is very promising, as this habitat is an integral part of the subterranean environment (Gers 1998) and has been proven to bring valuable discoveries in other parts of the world (Langourov et al. 2014; Mammola et al. 2016; Ortuño et al. 2023). Apart from undoubtedly critical taxonomic studies, some fundamental questions in subterranean biology worth pursuing are related to the ecology of cave organisms and their adaptation to the environment. Particularly interesting topics could be related to the ecosystem services of subterranean communities and their functional diversity (Mammola et al. 2020).

The Barra Honda National Park is an excellent example of successful cave and karst conservation in Costa Rica. This national park was created primarily to protect the unique karstic landscape (Goicoechea 2015), and the subterranean sites within its borders were well preserved. However, most of the subterranean sites in the country are located outside protected areas, indicating severe challenges to their conservation. The Zona Sur karst area, which consists of an extensive karst surface with the most significant number of caves in the country (Ulloa 2011), lacks state protection. In addition, most cave-dwelling species lack legal protection. For example, all bat species in our database are stated as Least Concern in the global IUCN red list because of their wide distribution. However, they may be locally rare, particularly because cave-dependent

species are vulnerable to disturbances in their roosts. Some of the country's most crucial subterranean bat roosts, Corredores, Gabinarraca, Damas, and Emus, lack any state of protection. Cave ecosystems are particularly vulnerable to anthropogenic threats such as pollution, disturbance due to tourist activities, and climate change (Mammola et al. 2019). With the rapid development of tourism and speleological activities (Ulloa and Goicoechea 2013), it is essential to preserve and protect the subterranean habitats and unique species assemblages that inhabit these sites. Understanding the unique adaptations and survival strategies of subterranean organisms will provide crucial data for developing effective conservation strategies to preserve fragile ecosystems.

Conclusions

Although the Costa Rican subterranean fauna has been the subject of a limited number of studies, our review and research have shown the current state of knowledge on the biodiversity of one-third of the known subterranean sites in the country. However, compared with cave-dwelling fauna from cave systems in other countries in the region, such as Belize, Guatemala, and Venezuela, we can infer that it is likely that a large number of Costa Rican subterranean organisms are yet to be described and reported within Costa Rican caves. Finally, with the current work, we hope to inspire and encourage future studies to focus on the exploration and documentation of new species in the underground habitats of the country.

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Supplementary material I

Dataset of cave-dwelling organisms occurring in Costa Rica

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Data type: xlsx

Explanation note: The dataset includes information on taxonomic diversity, location, protected areas, conservation status, and references.

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